RECRUITMENT AND EXPLOITATION OF GULF MENHADEN, *BREVOORTIA PATRONUS*[1]

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ABSTRACT

Gulf menhaden, *Brevoortia patronus*, range along the Gulf of Mexico coast from Cape Sable, Florida, to Veracruz, Mexico, and are exploited by a purse seine fishery from Alabama to eastern Texas. Rates of exploitation, population movement, and recruitment into the fishery were estimated from returns of tagged juveniles and adults. The annual instantaneous rate of natural mortality (M = 1.0935) was estimated from recoveries of tagged adults. Recruitment patterns were determined and exploitation rates were estimated from returns of fish tagged as juveniles in specific geographic regions along the northern Gulf of Mexico. During 1971-73, fish tagged as juveniles from either the eastern or western extremes of the northern gulf coast were exploited as 1-year-olds at a mean rate of only 5%. The rate increased to a high of 51% for 1-year-olds tagged near the Mississippi Delta, the center of the fishery. During 1972-74, 2-year-old fish tagged as juveniles were exploited at rates ranging from 18 to 55%. Fish from the eastern and western ends of the range dispersed toward the center of the range as they grew older.

Gulf menhaden, *Brevoortia patronus*, range along the coastline of the Gulf of Mexico from Cape Sable, Fla., to Veracruz, Mex. (Reintjes 1969). They are exploited from April to October by a purse seine fishery that operates in nearshore waters from Alabama to Texas. Gulf menhaden move offshore in the fall before spawning in the winter. The larvae move into estuaries in late winter and spring, where they metamorphose into juveniles and remain there until the following autumn.

The fishery is dependent on age-1 and age-2 fish, with few fish being taken that exceed 3 yr of age. The catch, processed into meal and oil, increased from 8,900 t in 1946 to 728,500 t in 1971, and has fluctuated between 447,000 and 820,000 t since then. Yellowfin menhaden, *B. smithi*, and finescale menhaden, *B. gunteri*, occur in the area fished, but Gulf menhaden compose approximately 99% of the landings. At present, catches are processed at 11 reduction plants, located at six ports along coastal Louisiana and Mississippi (Figure 1). Large, refrigerated purse seine vessels, supported by spotter aircraft, range up to about 320 km from port. During recent years the number of operating plants has varied from 10 to 13, and the number of active ports has varied from 6 to 8 (Nicholson 1978).

To determine if fish reared outside the range of the fishery are exploited and to determine the rate of exploitation of individuals reared within the range, juvenile menhaden (young-of-the-year) have been tagged since 1970 in selected estuaries from Florida to the Mexican border. I analyzed returns from fish tagged as juveniles from 1970 to 1972 to determine if fish reared outside the range of the fishery contribute to landings and to estimate rates of exploitation by age and estuarine area of origin.

I also analyzed returns from a second (independent) adult tagging program to obtain an estimate of natural mortality and a preliminary estimate of rate of fishing on fully recruited fish to complement my analysis of the first (juvenile) tagging program. In the second study, reported by Pristas et al. (1976), Gulf menhaden were tagged as recruited fish (adults) on the fishing grounds from 1969 to 1971.

TAGGING METHODOLOGY

Since all tags that are recovered from both tagging programs are from "adult" fish caught by the fishery, a distinction in terminology is made in this paper for clarity in separating results: "tagged as adults" or "adult recoveries" refers to the study reported by Pristas et al. (1976) and "tagged as juveniles" or "juvenile recoveries" refers to the present study.

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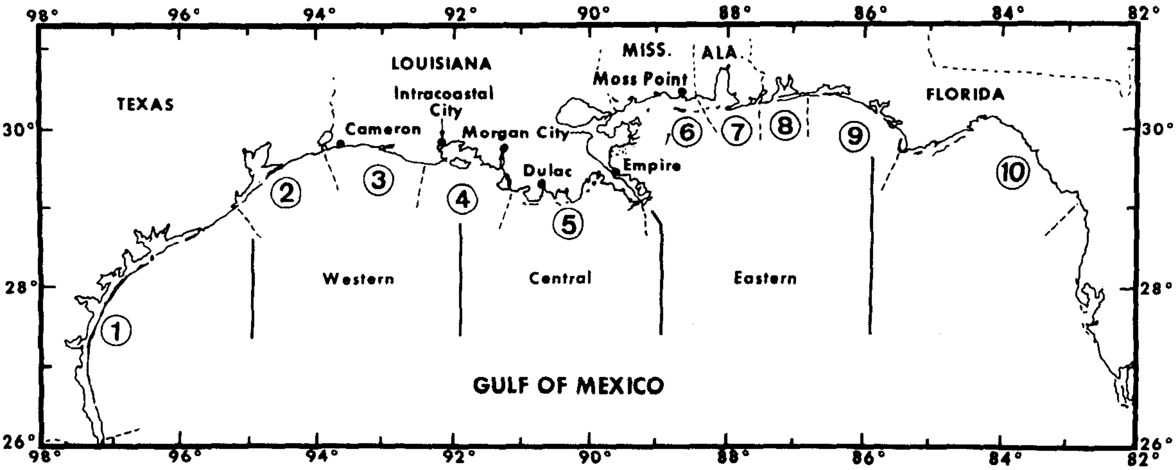

FIGURE 1.—Location of Gulf of Mexico ports where catches of Gulf menhaden are currently landed (dots), major fishing and tagged adult release areas (vertical lines), and division of the U.S. gulf coast into tagged juvenile Gulf menhaden release areas (numbered circles and dashes).

Methods of tagging and tag recovery are well documented (Pristas and Willis 1973; Parker 1973; Dryfoos et al. 1973). Numbered stainless steel ferromagnetic tags, 7.0 × 2.5 × 0.4 mm for juveniles, and 14.0 × 3.0 × 0.5 mm for adults, were injected into the body cavity. Juveniles were tagged in estuaries during late summer or early fall just before emigration. Adults obtained from fishing vessels on the fishing grounds were tagged during late spring.

Tags were recovered on magnets located in reduction plants; however, not all tags that entered a plant were recovered. To estimate the fraction of tags recovered at each plant, 100 tagged fish were put in the catch of a selected vessel each week. Field recoveries were adjusted for loss rates within a plant by multiplying the inverse of the test recovery fraction by the number of field tags actually recovered at each plant.

For analyzing juvenile tag recoveries, the northern Gulf of Mexico coast was divided into 10 release areas, numbered, and geographically named for reference (Figure 1, Table 1). In some areas, fish were tagged in only one estuary; in other areas, they were tagged in several estuaries. For analyzing adult tag recoveries, the coast was divided into three areas: western, central, and eastern (Pristas et al. 1976) (Figure 1).

TABLE 1.—Numbers of tagged juvenile Gulf menhaden released in estuarine waters by area and year, 1970-72. Areas are depicted in Figure 1.

Release area	1970	1971	1972
1. Southeast Texas	3,199	3,263	3,900
2. Galveston Bay	892	1,200	1,000
3. Western Louisiana	1,000	2,500	2,500
4. Central Louisiana	—	1,500	640
5. Western Delta	200	600	1,200
6. Eastern Delta-Mississippi	1,622	1,248	1,800
7. Mobile Bay	1,199	2,500	—
8. Pensacola Bay	600	1,000	1,700
9. Choctawhatchee Bay-St. Andrew Bay	—	200	2,482
10. Apalachee Bay	—	400	100
Total	8,712	14,411	15,322

MOVEMENT AND RECRUITMENT OF JUVENILE TAGGED FISH

The eventual distribution of fish tagged in specific estuaries would be an indication of the degree and direction of movement of fish from each estuary. Because there is no way of knowing exactly where a tagged fish was caught, and because levels of effort may vary between ports (and thus numbers of fish actually landed), the distributions must be inferred from estimates of the relative availability of tagged fish to each port rather than from just the distribution of recoveries of tagged fish to each port. Because vessels tend to fish more intensively in areas near their home ports, most tags recovered at a specific port were assumed to have been from fish caught in waters closest to that port. The measure of standardized effort (f') used in availability calculations is the vessel-ton-week (computed as net-registered-tonnage times number of weeks fished), the unit of fishing effort currently employed for this fishery (Chapoton 1972; Schaaf 1975), adjusted for differences in vessel catch efficiency in numbers of fish between ports and between years. (Landing and effort data from a former plant at Sabine Pass, Tex., were combined with Cameron, La., data for 1971.) This adjustment, made by multiplying the actual effort by the ratio of actual catch per unit effort in numbers of individuals to the overall port's and year's mean catch per unit effort (in numbers), makes all measures of effort by port equivalent with respect to numbers of fish landed.

Relative availabilities were calculated for juveniles tagged in nine specific areas from 1970 to 1972. No tags were recovered from fish tagged in area 10, probably because so few were tagged. For each of six ports, the estimated number of tags recovered annually from fish tagged in specific areas was divided by the number of tags recovered at all ports over all years. The quotient was divided by the amount of standardized fishing effort for the port during the year considered, and a three-dimensional matrix of relative availabilities by age of capture, port, and year class was calculated for each release area. The equation used for these calculations is:

$$\overline{RAV}_{ijk} = (R_{ijk}/\sum_i \sum_j R_{..k})/f'_{jm} \qquad (1)$$

where f'_{jm} = standardized effort,
R_{ijk} = number of recoveries, and
$\overline{RAV}_{ijk}$ = relative availability to a unit of effort.

Here, i refers to age at capture, j refers to port, k refers to year class, and $m = k + i$ (year captured).

The relative availability estimates at the different ports for each release area were similar between year classes and so were averaged for all years (Figure 2). These results support the hypothesis advanced by Kroger and Pristas (1975) that there is little or no exchange of fish between areas east and west of the Mississippi Delta. Large numbers of fish tagged east and west of the delta were recovered at Empire, La., plants; since vessels from these plants fish both sides of the delta there is no way of knowing on which side fish bearing these tags were actually captured. The few tags recovered at plants east of the delta of fish tagged west of the delta may actually have been taken by vessels from plants east of the delta fishing west of the delta, and vice versa. It is noteworthy that of the few tags recovered at plants west of the delta of fish tagged east of the delta nearly all were recovered at Morgan City and Dulac, La. Vessels from these ports were more likely to have fished east of the delta than were vessels from the two most western ports, Intracoastal City and Cameron, La. Almost no fish tagged east of the delta were recovered at these ports.

As fish age, there appears to be a slow dispersal toward the delta of fish from eastern and western areas. Fish tagged in the two most western areas were captured in greater numbers their second year after release at the two more central ports, Morgan City and Dulac. Although the fish tagged in the other three western areas were captured in greatest numbers their first year after release, they became progressively more available as 2-yr-olds to the three central ports than they were to the most western port at Cameron. However, 1-yr-old fish from these three western areas (3, 4, and 5) were disproportionately more available to the western extreme of the fishery than to the more central area. Fish tagged in the three most eastern areas were captured in greater numbers the second year after release at the Moss Point, Miss., and Empire plants. Fish tagged in the eastern area adjacent to Moss Point, although captured in greater numbers the first year after release, appeared to be more available as 2-yr-olds to Empire vessels than to Moss Point vessels.

As a consequence of the fishery being concentrated in Mississippi and Louisiana waters, fish reared as juveniles in the extreme eastern (Alabama and Florida) and western portions (Texas to the Mexican border) of the range are recruited at a lesser rate than fish reared in the center of the range. Fish moving toward the center of the range probably are recruited progressively later in the season as age 1, and many may not be recruited until age 2, whereas nearly all fish reared in the center of the range probably are recruited early in the season at age 1.

The gradual shift toward the center of the fishing area as a year class ages, indicated by the pattern of juvenile tag recoveries, is also indicated by the age composition of the catches. Age-1 fish compose a higher percentage of catches at plants or longitudes at the eastern and western ends than at plants or longitudes in the center (Nicholson 1978). The observed age composition is not due to greater fishing pressure on fish at either end of the fishing grounds, since attrition rates of fish tagged in the more central areas, implied by catch curves of tag recoveries, are equal to or greater than rates observed for fish tagged in either extreme (Figure 3). This shifting is apparently superimposed over

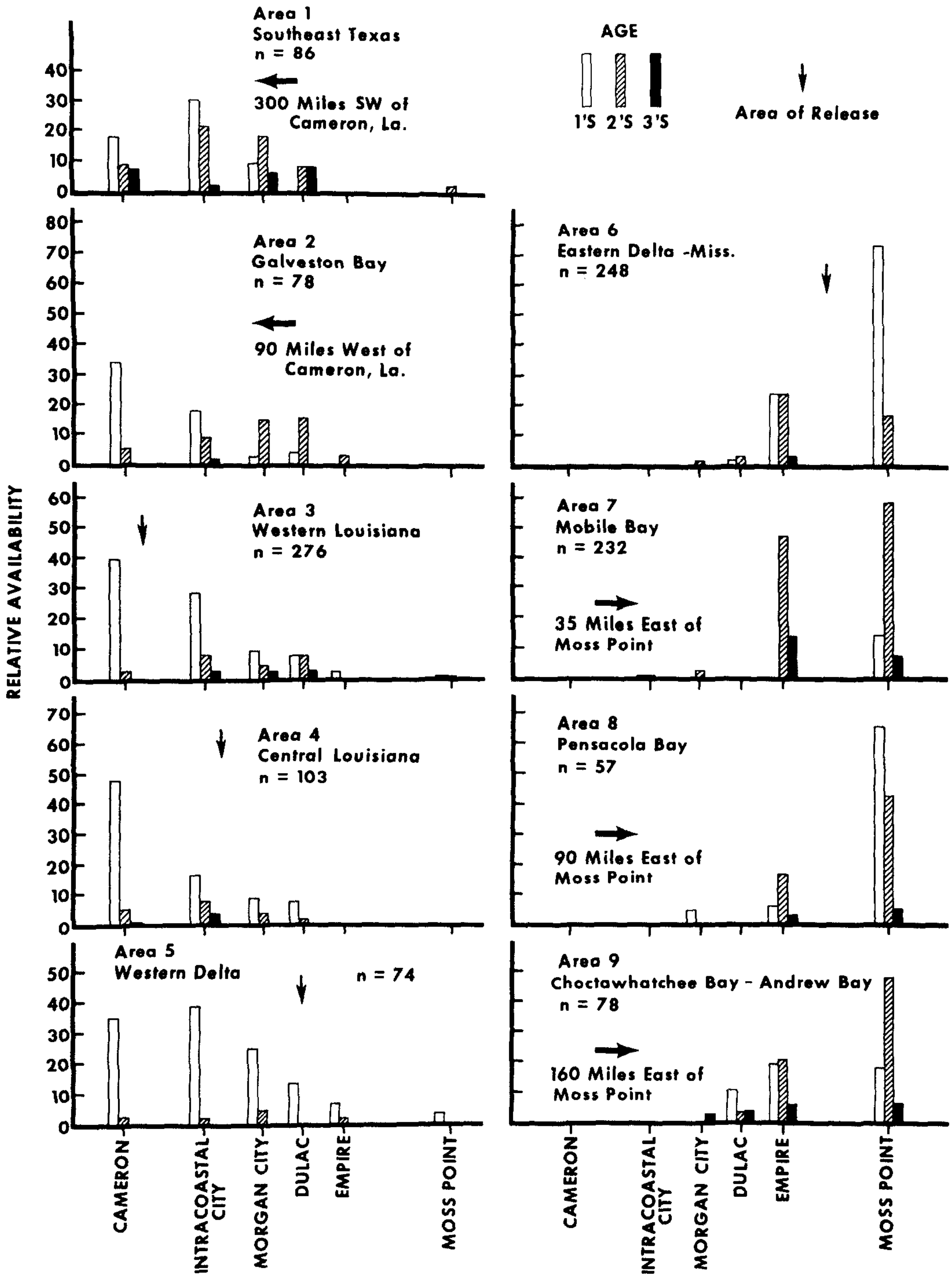

FIGURE 2.—The mean release area-specific availability by age of Gulf menhaden tagged as juveniles to individual ports in the Gulf of Mexico. Vertical arrows denote approximate release location with respect to the ports, horizontal arrows denote release locations beyond the range of the figure. The actual (unadjusted) number of tag returns is given for each release area.

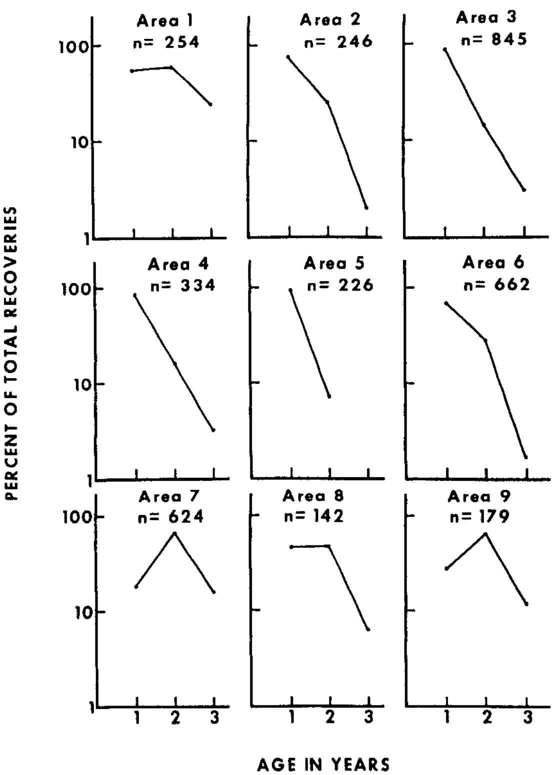

FIGURE 3.—The frequency of recoveries for a standard 100 tags for each juvenile Gulf menhaden release area (ordinate logarithmically scaled) and the adjusted number of recoveries from each release area, Gulf of Mexico.

an annual fall-spring, offshore-onshore migration (Roithmayr and Waller 1963).

The lack of precise recapture location information and the limited range of the fishery relative to the range of the species prevents the formulation of a more detailed and possibly more accurate description of dispersal patterns of Gulf menhaden. For instance, it is possible that fish from nursery areas outside the fishing grounds disperse at a more or less equal rate towards and away from the fishery. However, the relatively strong showing of tags from outside the fishery 2 and 3 yr after release and the relatively few schools of Gulf menhaden that are sighted at the extremes of the range indicate that dispersal is probably stronger towards the center of the range, where the fishery is heaviest, rather than away from it.

MORTALITY RATE ESTIMATION FROM ADULT TAG RECOVERIES

To estimate the age specific exploitation rate of Gulf menhaden from different geographic nursery areas, I needed an estimate of the instantaneous natural mortality rate (M) and an estimate of the exploitation rate (u) of fully recruited fish. I used the tag recovery data from the adult tagging study reported by Pristas et al. (1976) to estimate these parameters, because these fish (being obtained from commercial purse seine sets) were assumed to be fully recruited when tagged, and the adult tagging study is independent from the juvenile tagging study which will be used as the data base for the area and age specific exploitation estimation. Before mortality rates were estimated, however, adjustments were made to the adult tag-recovery data to remove the potential for systematic errors in the results.

A, B, and C errors (Ricker 1975) are commonly associated with tagging studies attempting to estimate rates of survival and fishing. Type A errors can occur when tagged fish die as a result of marking or shed their tag shortly after tagging and also during the recovery phase when reporting of recoveries is incomplete (in this case loss of tags within a reduction plant). Type A errors are characterized by affecting estimates of rate of fishing (hence rate of natural mortality) but not rates of total mortality when these parameters are estimated by rates of recovery over several time intervals.

Adjustments of numbers recovered for incomplete recovery of tags from harvested tagged fish is straightforward and is outlined in the Tagging Methodology section. Adjustments of numbers released entailed adjusting for any significant difference in recovery rates associated with different taggers and then determining a realistic estimate of rate of loss due to death and shedding shortly after tagging, which is applicable to all taggers. Since only three taggers were employed in this study, and one only tagged 200 fish in 1971, a recovery comparison was conducted between the two taggers who tagged the greatest number (99.7%) of the fish. Because the recovery rate for fish tagged by one individual (tagger B) was much lower than the rate for fish tagged at the same time by the other (tagger A) (Table 2), the number of tags applied during 1969 by this tagger was adjusted downward. The adjustment was made by multiplying tagger B's number released for each area by the ratio of the recovery rate of tagger B to tagger A for each area. All of the remaining releases (1970 and 1971, with the exception already noted above) were tagged by tagger A. Adjusted recov-

TABLE 2.—Comparison of differences in recovery rates between taggers for paired tagging of adult Gulf menhaden conducted in 1969 in the Gulf of Mexico. All chi-square values obtained from 2×2 contingency tables were highly significiant ($P < 0.001$).

Area	Tagger	No. tagged	Actual recoveries	Chi-square
Eastern	A	6,700	1,118	77.05
	B	6,300	713	
Central	A	1,900	402	36.54
	B	1,800	245	
Western[1]	A	4,100	456	120.04
	B	3,700	163	

[1]Release totals in Table 3 contain an additional 2,500 tags released by tagger A working alone.

eries and numbers released with adjustments for differential tagger induced mortality (1969 only) for the adult study are given in Table 3. (The number of adjusted recoveries differs from the number published by Pristas et al. (1976), probably because slightly different methods were used to adjust known recoveries and somewhat different criteria were used to judge the suitability of some returns.)

Adjustments of numbers released to account for tags lost from initial mortality and shedding had to be somewhat arbitrary. Kroger and Dryfoos (1972) reported on a series of short-term tagging mortality and shedding studies on Atlantic menhaden, *B. tyrannus*, which tested a variety of methods of insertion, fish size, chemical treatment of tags, and tag size. Of this series, two were with fish size and tagging methodology similar to the Gulf adult study. Losses due to mortality and initial shedding in these two experiments were 10 and 24%. Since these experiments were conducted under better conditions than field tagging, I selected a value nearer the higher of the two estimates, 20%, as a realistic mean rate of Type A tag loss, and 10-30% as a range for testing the sensitivity of this assumption.

Type B errors can occur when tags are shed throughout the recovery period, when tagged fish have a higher rate of mortality, or when tagged fish emigrate from the fishing grounds. Errors of this type will cause overestimation of total mortality and natural mortality but not necessarily rate of fishing. No corrections were made for Type B errors because no long-term studies of shedding or mortality under this category have been conducted with menhaden. Since tagging wounds heal within a few weeks after tagging (Kroger and Dryfoos 1972) and the internal tag is stainless steel with rounded, smooth edges, I would expect Type B losses to be minimal. Emigration from the fishing grounds is unlikely (see Recruitment section above).

Type C errors occur when the tagged individuals are either more or less susceptible to capture than untagged fish during the first year after release. Recovery rates for later years may be representative, however. Adjustment for Type C error is made in the estimating method, as will be shown later.

The Gulf menhaden tag-recovery data are subject to an additional type of error. Sometimes tags from recaptured fish lodged in plant machinery and were not recovered until 1 or more years after entering a reduction plant (Table 4). The retention of tags in plants for more than one season prior to their recovery will cause estimates of total mortality to be too low. Since trial calculations (of simulated data) showed that the rates of tag retention noted would cause underestimation by only about 5.4% for fish marked with large (adult) tags and 3.8% for fish marked with small (juvenile) tags, and attempts to adjust for this bias may introduce additional error, the effects were ignored. [Tag retention rates were not as large as reported by Nicholson and Schaaf (1978). The most serious discrepencies were for two plants during 1972, where retention rates were reported as 5 and 6%. It was discovered that 34 of the 59 tags reported as retained for 1 yr in one plant and 92 of the 93 tags reported as retained in the other plant were erroneously recorded. Corrected retention rates are 2 and <0.1% for the two plants.]

Plots of log frequencies of adult recoveries for each release year and area (Table 3) on years-at-

TABLE 3.—Number of adult Gulf menhaden tagged in late spring, by area, year, and adjusted number recovered, Gulf of Mexico.

			No. recovered in year			
Area	Year	No. tagged	1	2	3	4
Western Gulf	1969	[1]8,065	1,363	509	68	6
	1970	9,100	3,619	838	15	4
	1971	7,400	2,622	235	24	1
Central Gulf	1969	[1]3,056	1,311	215	21	—
	1970	5,100	2,168	408	22	—
	1971	5,200	1,617	94	11	6
Eastern Gulf	1969	[1]10,965	2,305	1,123	134	22
	1970	3,575	1,315	321	33	7
	1971	10,200	2,694	742	89	9

[1]Adjusted for tagger induced mortality.

TABLE 4.—Mean percentage of large (adult) and small (juvenile) test tags recovered in Gulf menhaden reduction plants, Gulf of Mexico.

Tag type	Release years	Percentage recovered in season of release	Percentage recovered in seasons after release		
			1st	2d	3d
Large	1969-71	51	0.56	0.05	0.02
Small	1970-72	34	.38	.02	.01

large indicate that mortality rates were generally similar for all areas and years (Figure 4). Since not all areas and years had 4 yr of recoveries, and two of the three areas did not have strongly linear plots (hence a constant annual Z) for 1970 releases, I selected the more linear 3 yr of recovery data from each area for 1969 and 1971 for further analysis (points joined by solid lines on Figure 4). Based on the plotted data of Figure 4, I assumed that Z (hence survival and rate of fishing) was constant for years 1-3 following release for the western area in 1971 and the central area in 1969 and 1971. I assumed a Type C error condition for the first year after release for the western area in 1969 and the eastern area in 1969 and 1971 and assumed Z to be constant for years 2-4 in these three data sets. I also assumed that all the fish tagged as adults, which were released in late spring just after fishing had begun, were subjected to a full season of natural mortality.

I used the slope of a weighted regression of the natural logarithms of recoveries on years-at-large where mortality was assumed constant as an estimate of Z. Each regression point was weighted by the number of unadjusted recoveries that provided the basis for that point.

For release groups with an estimate of constant Z for years 1-3, called here Z_1, the constant annual exploitation rate (u_1) was estimated directly by (Ricker 1975):

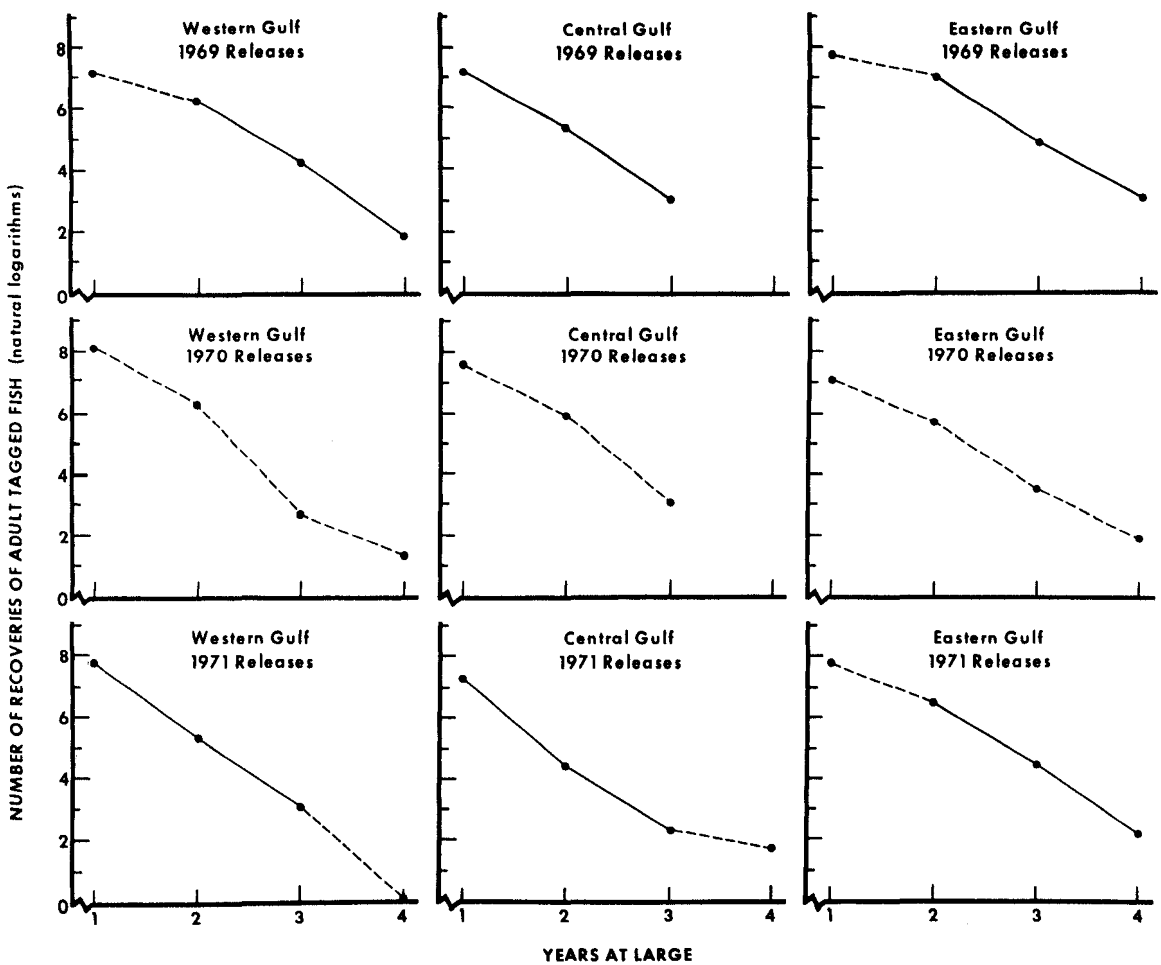

FIGURE 4.—Natural log frequency of recoveries by years at large for tagged adult Gulf menhaden by fishing area and release year, Gulf of Mexico. Lines connect points used to estimate instantaneous total mortality rate (Z) (assumed constant for 3 consecutive years), and dashes connect points not used in the estimation procedure for Z.

$$u_1 = \frac{R_1 + R_2 + R_3}{M'(1 + S_1 + S_1^2)} \quad (2)$$

where M' = the number tagged and released, adjusted for tagging loss,
$S_1 = e^{-z}$, the constant annual survival rate, and
R_n = number of adjusted recoveries for years-at-large n.

For release groups with an estimate of constant Z for years 2-4, called here Z_2, the constant exploitation rate (u_2) had to be estimated by trial, since the rate for the first season could not be assumed a constant for later years (Type C error condition). A trial value of Z_1 for the first year-at-large also provided first year trial values of S_1 and A_1 (total annual mortality rate); u_2 was estimated for the second and later years-at-large by (Ricker 1975):

$$u_2 = \frac{R_2 + R_3 + R_4}{S_1 M'(1 + S_2 + S_2^2)} \quad (3)$$

and also by:

$$u_2 = \frac{A_2}{Z_2}\left(Z_2 - Z_1 + \frac{R_1 Z_1}{M' A_1}\right). \quad (4)$$

The trial value of Z_1 was adjusted until Equations (3) and (4) converged on virtually equivalent estimates of u_2.

The annual instantaneous rate of fishing mortality (F) was estimated by:

$$F = \frac{uZ}{A} \quad (5)$$

where $A = 1 - e^{-z}$, the total annual mortality rate, and u, Z, F, and A are subscripted 1, where Z was constant through years 1-3, and 2 where Z was constant through years 2-4.

The annual instantaneous rate of natural mortality (M) was estimated by:

$$M = Z - F \quad (6)$$

where, as above, Z and F are subscripted 1 for constant mortality years 1-3 and 2 for constant mortality years 2-4.

The central area had the greatest variation in parameter estimates between years, while the western area had the least (Table 5). I averaged all estimates of M and u for each tagging loss rate examined to obtain unweighted means (Table 6). A change in the estimate of tagging loss resulted in a slightly greater than 1:1 fractional change in the estimates of M and u.

TABLE 5.—Estimated annual instantaneous natural (M) and fishing (F) mortality rates and exploitation rates (u) for tagged adult Gulf menhaden in the Gulf of Mexico, assuming a 20% initial tag loss to shedding and mortality.

Area	Year	M	F_1	F_2	u_1	u_2
Western Gulf	1969	1.1672	—	0.9300	—	0.3890
	1971	1.2287	1.1665	—	0.4426	—
Central Gulf	1969	.6927	1.2043	—	.5396	—
	1971	1.6083	1.1367	—	.3875	—
Eastern Gulf	1969	.8805	—	1.1673	—	.4965
	1971	.9835	—	1.1662	—	.4793

TABLE 6.—Estimates of mean annual rate of exploitation (u) and instantaneous natural mortality rate (M) for Gulf menhaden in the Gulf of Mexico, estimated from recoveries of tagged adults, with varied levels of tagging mortality.

	Tagging loss rate				
Parameter	10%	15%	20%	25%	30%
u	0.4122	0.4328	0.4558	0.4815	0.5106
M	1.2019	1.1506	1.0935	1.0293	0.9568

Since the earlier estimates of each Z were from weighted regressions with only three data points and hence only one degree of freedom for estimating confidence intervals (C.I.), I conducted a combined analysis of scaled data for the six sets of release-recovery data for 1969 and 1971 (which consist of 18 data points and, hence, 16 df) to determine the stability of the estimate of M relative to the variance about the estimate of Z. After scaling the data, each release-recovery set summing to 10,000, I estimated the unweighted predictive regression slope estimate of Z_2 and its 95% C.I. by standard methods (Draper and Smith 1966). Assumptions on which years represented periods of constant total mortality were the same as for the earlier analysis. Equations (3) and (4) were used to estimate u_2 from the scaled estimate of Z_2 and for the high and low extremes of the 95% C.I. F_2 and M were estimated by Equations (5) and (6) as before. The resulting estimate of M and its approximate 95% C.I., although slightly lower than the earlier estimate, represent very similar values, and relative to the variance about the estimate of Z_2, M is quite stable (Table 7).

To determine if the arbitrary selection of 3 yr of recovery data for analysis, adjustment for Type C error, and use of weighted regressions had a major altering effect on the resulting estimate of M, I estimated M using all recovery data points for the

TABLE 7.—Estimates from scaled data of total annual instantaneous mortality rate (Z_2), rate of exploitation (u_2), instantaneous fishing mortality (F_2), instantaneous natural mortality (M), and their approximate 95% confidence intervals (C.I.), for Gulf menhaden tagged as adults in the Gulf of Mexico.

Parameter	Estimate	High 95% C.I. limit	Low 95% C.I. limit
Z_2	2.2241	2.4356	2.0126
u_2	0.4692	0.5041	0.4307
F_2	1.1701	1.3456	1.0005
M	1.0540	1.0900	1.0121

1969 and 1971 releases, no Type C correction, and an unweighted predictive regression estimate for Z. The resulting mean estimate for M, 1.0852, is very similar to the estimate of M, 1.0935, obtained from the more refined analysis. Inclusion of the 1970 release-recovery data in this analysis resulted in a somewhat lower mean estimate of M, 1.0089. The lower M estimates for the 1970 releases probably resulted from a lower rate of tagger induced mortality than for the 1969 and 1971 release groups, as the 1970 tagged fish were larger than the fish tagged during the other 2 release years.

As evidenced by the similarity of results from the two modified analyses and the results depicted in Table 6, the estimate of M is apparently more sensitive to the correction factor for tagging mortality loss than the estimates of other parameters used in its estimation. Unfortunately, data on the nature of the statistical distribution on which to base variance estimates and hence approximate 95% C.I. are lacking. Based on the current knowledge of tagging mortality for menhaden, the estimates obtained for a 20% tagging loss and the weighted regression technique (M = 1.0935 and u = 0.456) are the best estimates currently available.

AREA-SPECIFIC AND AGE-SPECIFIC EXPLOITATION RATES

To estimate area-specific and age-specific exploitation rates from recoveries of tagged juveniles, it is necessary to estimate the number of tagged fish alive at the beginning of each fishing season. These numbers can be estimated from the number of recoveries by sequential analysis (Ricker 1975). The data and parameters needed are the number of recoveries (R_n) by age (n), an estimate of M, and an estimate of u for a given cohort during its last year in the fishery.

The numbers of tags recovered in all years for fish released in specific areas were pooled by age of capture and, with one exception, were unweighted (Table 8). For three estuaries, which constituted the southeast Texas area, the recoveries were weighted so that each estuary contributed equally to the totals.

TABLE 8.—Area-specific annual exploitation and fishing mortality rates estimated by sequential analysis of recoveries of tagged juvenile Gulf menhaden in the Gulf of Mexico. Numbers in parentheses are initial rates of exploitation obtained from the analysis of adult-tagged fish.

Area	Age	N_n	u	F	S	R_n
1. Southeast Texas[1]	1	2,557	0.050	0.086	0.3074	129
	2	786	.184	.348	.2366	145
	3	186	(.456)			85
2. Galveston Bay	1	656	.270	.549	.1935	177
	2	127	.505	1.351	.0868	65
	3	11	(.456)			[2]5
3. Western Louisiana	1	2,096	.338	.737	.1603	709
	2	336	.330	.715	.1639	111
	3	55	(.456)			25
4. Central Louisiana	1	763	.373	.843	.1442	284
	2	110	.390	.901	.1361	43
	3	15	(.456)			7
5. Western Delta	1	412	.509	1.373	.0849	210
	2	35	(.456)			16
6. Eastern Delta-Mississippi	1	1,748	.265	.538	.1956	464
	2	342	.547	1.563	.0702	187
	3	24	(.456)			11
7. Mobile Bay[3]	1	3,896	.027	.045	.3203	105
	2	1,248	.343	.753	.1578	429
	3	197	(.456)			90
8. Pensacola Bay	1	587	.112	.200	.2743	66
	2	161	.417	.992	.1242	67
	3	20	(.456)			9
9. Choctawhatchee Bay-St. Andrew Bay	1	977	.049	.084	.3080	48
	2	301	.368	.830	.1461	111
	3	44	(.456)			20

[1]Weighted recoveries for this subarea only.
[2]Pooled age-3 and age-4 recoveries.
[3]Estimates are unrealistic; see Table 9 and text.

The number of tagged fish alive (N_n) in their last representative year in the fishery at the beginning of a fishing season was estimated by:

$$N_n = \frac{R_n}{u} \tag{7}$$

where u = 0.456 from the adult tagging analysis.

An estimate of S_{n-1} was required to estimate the number of 2-yr-old tagged fish alive (N_{n-1}) at the beginning of a fishing season from the equation:

$$N_{n\text{-}1} = \frac{N_n}{S_{n\text{-}1}}. \tag{8}$$

S_{n-1} was estimated by substituting trial mortality estimates (assuming M = 1.0935) into the following equation until the right side equaled the number of recoveries at age $n - 1$ (Ricker 1975):

$$R_{n-1} = N_n \left[\frac{F_{n-1} A_{n-1}}{S_{n-1} Z_{n-1}} \right]. \quad (9)$$

By repeating this procedure, Equations (9) and (8), using N_{n-1} as an estimate of 2-yr-olds alive at the beginning of a fishing season, the number of tagged 1-yr-olds (N_{n-2}) alive at the beginning of a fishing season was estimated.

Age (n) specific exploitation rates were estimated for each release area by using the estimated age specific mortality rates in:

$$u_n = \frac{F_n A_n}{Z_n}. \quad (10)$$

Except for fish tagged in the Mobile Bay, Ala., area (Alabama coastal waters are closed to purse seining) the exploitation rates for both age-1 and age-2 fish declined progressively as the distance from the delta increased. The decline was much greater for age-1 than for age-2 fish (Figure 5). The low rates of entry of fish from the extremes of the range and the purse seine closure imposed for coastal Alabama waters may enable a small buffer stock to survive in the event of heavy exploitation.

For fish tagged in Mobile Bay, the number estimated to have been alive at the beginning of the first fishing season exceeded the number of fish tagged, an obvious impossibility (Table 8). In outside waters, Gulf menhaden are taken incidentally by the industrial bottom trawl fishery (Roithmayr and Waller 1963) and by the shrimp fishery in inside and outside waters. The overestimate of N_1 may have been the result of estimated M being too high for this group of fish. One possibility for M being too high is that the loss of tagged fish to other causes, which is included in the estimate of M, may be lower than for fish tagged in all other areas.

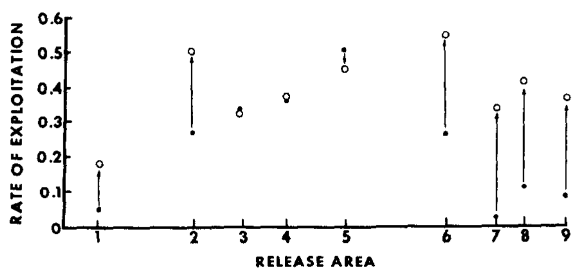

FIGURE 5.—The rate of exploitation by release area for age-1 (dots) and age-2 (circles) Gulf menhaden tagged as juveniles in estuaries on the Gulf of Mexico. Arrows indicate degree and direction of change between years.

Estimates of initial tag loss from shedding and death were made by comparing the number of fish estimated to have been alive at the beginning of the first season with the number that should have been alive if only natural mortality (M = 1.0935) had caused deaths during the approximately 8 mo (0.67 yr) following tagging. The apparent tagging loss estimates (L) were calculated by estimating the fraction by which M' would have to be reduced to equal N_1 prior to undergoing 8 mo of natural mortality, i.e.:

$$(M' - LM')e^{-0.67M} = N_1$$

by solving for L and simplifying,

$$L = 1 - \frac{N_1}{M'(e^{-0.67M})}. \quad (11)$$

The resulting estimates, expressed as a percentage of the number of fish tagged, ranged from 22.1 to 63.0% (Table 9). These estimates seemed realistic in view of the loss rates reported by Kroger and Dryfoos (1972) for Atlantic menhaden of similar size tagged with small (juvenile) tags. These estimates do not, however, have any bearing on the 20% tagging loss estimate used for the adult study, as this study used larger fish and larger tags.

TABLE 9.—Numbers of juvenile Gulf menhaden tagged in autumn, numbers estimated by sequential analysis to have been alive the following April, and effectual tagging loss rates, Gulf of Mexico.

Release area	Number tagged	Number estimated alive	Effectual tagging loss
1. Southeast Texas[1]	13,460	2,557	0.605
2. Galveston Bay	3,092	656	0.559
3. Western Louisiana	6,000	2,096	0.273
4. Central Louisiana	2,140	763	0.258
5. Western Delta	2,000	412	0.571
6. Eastern Delta-Mississippi	4,670	1,748	0.221
7. Mobile Bay[2]	3,699	3,896	—
8. Pensacola Bay	3,300	587	0.630
9. Choctawhatchee Bay-St. Andrew Bay	2,682	977	0.242

[1]Weighted data for this area only.
[2]Unrealistic results, see text.

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